Modelling Productivity of Willow Stands in Sweden

Evaluation of Concepts for Radiation Use Efficiency
and Soil Water and Nitrogen Availability

Angela Noronha Sannervik

Modelling productivity of willow stands in Sweden – evaluation of concepts for radiation use efficiency, and soil water and nitrogen availability.

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Abstract

The aim of this thesis was to answer the question: Which processes should be included in a model to simulate willow production as a function of climate, soil and fertilisation conditions?

Studies were carried out to determine: a) the radiation use efficiency of an unstressed willow stand; b) to which degree willow growth can be described as a function of absorbed radiation, shoot age and shoot mortality; c) to which extent model predictability is improved by further including soil water availability and d) nitrogen availability. Model simulations were tested against biomass production of 22 stands representing differences in location, soil type and fertilisation level.

It was found that radiation use efficiency varies with shoot-age. This was attributed to differences in canopy development, and to mortality caused by self-thinning. The absorbed radiation, shoot age and shoot mortality could explain 70 to 85% of the observed variations in stem biomass at harvest and 32 to 48% of the observed variations in annual production. Incorporating simulations of soil water availability decreased model predictability except for production of three-years-old shoots. Including simulations of soil water and nitrogen availability improved the degree of explanation in some situations. For all stands, model predictability of biomass at harvest was improved from $r^2 = 0.70$ to $r^2 = 0.82$ and of annual biomass from $r^2 = 0.70$ to $r^2 = 0.82$. For low or not fertilised stands, only a slightly improvement was obtained in explaining variations at harvest and none for variations of annual biomass. For fertilised stands, model predictability was decreased except for production of three-years-old shoots. Predictability of three-years old shoots production was improved, for all situations, by including simulations of soil water and nitrogen availability.

For willow stands growing on former arable land in southern Sweden, variations on biomass production at harvest, of stands with similar fertilisation level, can be simulated from the absorbed radiation and shoot mortality caused by self-thinning. Simulations of soil water and nitrogen availability are only worthy of including to explain yield variations of stands with different fertilisation levels. Variations in biomass production between years and sites are indicated to be poorly related to annual variations in solar radiation, shoot mortality or soil water and nitrogen availability.

Key words: drought, growth, model complexity, nutrition, *Salix viminalis*, willow coppice systems

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Noronha-Sannervik, A. & Kowalik, P. 2003. Annual variations in the solar energy conversion efficiency in a willow coppice stand. *Biomass and Bioenergy* 25, 227-233.
II. Noronha-Sannervik, A., Eckersten, H., Verwijst, T. & Nordh, N-E. Simulation of willow productivity based on radiation use efficiency, shoot mortality and shoot age. (Manuscript).
III. Noronha-Sannervik, A., Eckersten, H., Nyman, P. & Torssell, B. Modelling radiation use and water availability in willow forest in Sweden. (Manuscript).
IV. Eckersten, H., Noronha-Sannervik, A., Torsell, B. & Nyman, P. Modelling radiation use, water and nitrogen in willow forest. (Manuscript).

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Introduction

Background

The increasing demand for renewable energy sources combined with the need for alternative non-food crops lead to an increased interest for willow (Salix sp) coppice forests. Another area where the use of willow coppice is gaining interest is as vegetation filters for treatment of domestic wastewater (c.f. Aronsson, 2000). In Sweden the first experimental willow coppice stands, for fuel wood, were planted already in the 1970's. In the 1980's "appeared" the first commercial willow energy forests and an expansion of full-scale plantations took place in the early 1990's (Rosenqvist et al., 2000). With this expansion, willow stands were planted on new sites increasing the variability of the environmental conditions under which willow plantations were established.

A number of studies have been made to determine the expected biomass production for willow stands. Values reported from research fields in north Europe are normally in the range of 10 - 12 t ha^{-1} y^{-1} (e.g. Ettala, 1988; Christersson, Sennerby-Forse & Zsuffa 1993) and of 15 - 20 t ha^{-1} y^{-1} in southern Europe (c.f. Nixon et al., 2001). Cannell et al. (1987) estimated that potential biomass production from willow coppice, in southern England, could be 20 t ha^{-1} y^{-1}. In Sweden, estimations of potential production for *Salix* energy forests, made by Perttu (1983), show a range of variation from 10 to 20 t ha^{-1} y^{-1} in central and south Sweden. The estimations done by Cannell and Perttu were based on empirical relationships. Eckersten, Nilsson & Lindroth (1989) used a simulation model to estimate the willow potential production at various locations and weather situations in southern Sweden. The mean annual stem production obtained ranged from 6.5 to 10, 9 to 13 and 10 to 14.5 t ha^{-1} y^{-1} for 1, 2 and 3-year-old shoots, respectively.

The normal production levels, obtained from research fields, can be compared to what can be expected on private owned willow forests . The yields from the first harvests of commercial willow energy forests, in Sweden, were 30 to 40% lower than those projections (10-12 t ha^{-1} y^{-1}) (Host, Isebrands & Perttu, 1996). Economical calculations, done in the middle of the 90's, based on harvest chipping and transport costs as well as subsidies and willow biomass prices, indicate that production of energy forests needs to be above 8-10 t ha^{-1} y^{-1} (Johansson & Rosenqvist, 1995) to become profitable. Hence, the actual low harvest levels of around (7) t ha^{-1} y^{-1} may jeopardise future investments on willow energy forests.

A question is raised whether the lower production levels, obtained in commercial plantations, are a result of negligent management? The low production levels could be a result of establishment on sites not appropriated (soil and weather conditions) for willow growth. To focus the management the contribution of variations in environmental conditions to variability in production has to be estimated.

Thus, the lower production (in commercial plantations) than expected (from research fields) increased the awareness of the importance to understand and predict the effects of site conditions on willow production. Not only for a particular time but also having in mind that environmental conditions change with time, and that climate research predicts a systematic change in future.

It is not possible, experimentally, to test all combinations of environment conditions and management practices that may occur in the field (Isebrands et al., 1982). Modelling, however, can provide the means to predict numerous possible combinations. The requirement is that the model can be used outside the range of the conditions used in model development (Landsberg et al., 1991). A model based on important mechanisms of the system has that potential. Further, it is also important to avoid over simulation has this would imply supplemental data collection (Loague & Green, 1991) and, in practice, reduce applicability on privately owned fields. In this study the importance of some basic mechanistically based concepts is examined.

Pre-requisites for willow growth

The main factors having a continuous effect on willow growth are believed to be factors such as temperature, light, soil water and nitrogen (N) availability and intra-specific competition. While other factors such as, weeds, browsing, pests, diseases and frost, occur as events affecting willow growth during a limited period of time. In the particular case of weeds, they may be always present in the willow stands. However, their negative impact, on willow growth, is only significant during establishment and during the first growing season after harvest (Ford-Roberts, Mitchell & Watters, 1996; Sage, 1999).

In this thesis the first referred factors, of continuous character, are studied since it is the potential production of healthy willow stands, for a particular site, that is in focus.

According to Perttu (1983), air temperature is the most limiting climate factor for forest production in Sweden, since it determines the length of the growing season. To be favourable for intensive cultivation of willow forests, the growing season, needs to be above 160 days (Perttu, 1983). This implies that the favourable areas, for willow energy forests, in Sweden are located in the southern part (south of latitude 60 °N). The commercial willow plantations that are established today in Sweden are all within this area with favourable climate. Nevertheless, the actual length of the growing season can vary from year to year and from site to site within this area. Perttu (1983), determined that "the growing period normally lasts between 160 and 230 days" in southern Sweden. Thus, when modelling willow growth in southern Sweden it is important to consider the role of the temperature in determining the length of the growing season.

Other major factors considered to be important to take into account when modelling willow growth are light, soil water and nitrogen availability (Ågren, Kowalik & Perttu, 1989) and intra-specific competition (Tomé & Verwijst, 1996). However, their importance varies from site to site as the soil ability to provide the plants with water and nutrients, as well as management strategies, varies. One can ask, how important are the effects of soil water and N ability presupposing, for example, both, fertilisation and irrigation? In which cases does the influence of such factors, on willow growth, need to be included in a simulation model? In which cases can the expected production level depend on the interaction between the leaf area development and intra-specific competition?

Cannel et al. (1987) found that, for unstressed willow stands, the development of the leaf area is important to assure that a high fraction of the solar radiation, reaching the stand, is used by the plants to produce biomass. These authors estimated that for each week's delay in the start of canopy development, the potential stem production was reduced by 0.9 t ha^{-1} in a fertilised and irrigated willow stand. One way of achieving a rapid canopy closure is by planting at higher densities. However, a denser spacing of plantation also enhances intra-specific competition (Willebrand & Verwjist, 1993) leading to self-thinning which in turn leads to shoot and stool mortality (Verwjist, 1991). Shoot mortality, in turn, leads to the appearance of gaps in the stand canopy (Verwjist, 1996) decreasing radiation absorption.

For fertilised and irrigated willow stands, productivity seems to be dependent on the interaction between leaf area (determining radiation absorption) and intra-specific competition (leading to shoot mortality). However, irrigation and fertilisation are costly measures for the grower and therefore not widely used (particularly irrigation) in commercial willow plantations. In these cases, the natural ability of the soil to provide the plants with water and nutrients is determinant. Thus it is important to identify the manner and degree to which those factors constrain site biomass productivity.

Simulation of willow production

Several models have been developed to forecast biomass production of willow short-rotation forests and to study the effect of limiting factors on their growth (see Perttu & Kowalik, 1989 and Perttu & Philippot, 1996). In general, they range from simple growth and yield models that primarily use statistical analyses to describe data on growth and biomass production, to complex process-based models, that aim to predict the behaviour of the system under different environmental conditions.

As an example of a simple regression model can be referred Perttu's (1983) empirical relationship between temperature, latitude and willow potential production. This relationship was further developed by Morén and Perttu (1994), to include also altitude. Another example is the relationship between temperature and leaf area development used by Cannell et al. (1987), to determine potential production of unstressed willow stands. The advantage of this type of models is

that they are easy to use in practice, as they require little data. They can be used to identify areas with a favourable climate for willow growth but not to describe, for example, differences in biomass production in response to management practices, as they are limited in terms of feedback mechanisms.

A simulation model was applied by Nilsson & Eckersten (1983) to estimate the potential production of willow stands. This model, developed by Eckersten et al (1983), included several processes dealing with carbon dynamics in the plant (e.g. photosynthesis, respiration and allocation) and calculated annual production as a function of radiation and temperature. The model has undergone several improvements (see e.g. Eckersten, Lindroth & Nilsson, 1987) such as to include, for example, features for multiple-year simulations (Eckersten, Lindroth & Nilsson, 1989). The model is limited to situations with optimal water and defined nutrient supplies, which is seldom the case in commercial plantations.

Nitrogen supply is taken in consideration by Ågren (1989) in a growth model that is driven by nitrogen uptake in the plants. The external supply of nitrogen is connected to foliar biomass production, total biomass accumulation and turnover of nitrogen for a willow stand. The model can be used to investigate the effects of fertilisation on stand production but is lacking water dynamics.

Other authors explore the relationship between biomass production and water uptake and have simulated willow growth based on the water use efficiency concept (Lindroth & Båth, 1999). This simple water-limited yield model can be used to identify areas where precipitation levels are favourable for willow growth. However it assumes optimal nutrient supply and has no representation of soil. The soil is incorporated in an evaporation model developed by Halldin (1989) to simulate willow evaporation. The soil water is described in terms of a single compartment being the vertical distribution of water uptake in the soil ignored.

Persson & Jansson (1989) applied a multi-layered soil water and heat model that predicts water dynamics for a variety of soils and vegetation covers, to a willow stand. The upward and downward water flow between soil layers is considered and the model can be used to evaluate the effect of irrigation on willow growth. This model is known as SOIL model and it has been coupled to a model that simulates nitrogen dynamics in the soil and in the plant and plant growth (Eckersten & Slapokas, 1990). Together they constitute the SOIL-SOILN, a complex process-based model that has been used by Eckersten (1994) to simulate the growth of the first four years of a willow stand. The model, besides to include carbon and nitrogen dynamics in the plant, it also accounts for the influence of soil water and nutrient conditions. This is a comprehensive simulation model available for willow coppice stands (it can be used to other crops also) and its major limitation is the large amount of data required.

In the last decade, an increasing number of models that integrate both empirical and mechanistic elements at the same hierarchical level have been developed. As examples of such type of models developed for forest systems, we find BIOMASS (McMurtie et al., 1994) for *Pinus radiata* and *Eucalyptus* spp., 3-PG (Landsberg

& Waring, 1997) for *Picea sitchensis* and PROMOD (Battaglia & Sands, 1997) for *Eucalyptus globulus*. These models are based on the radiation-use efficiency concept, i.e., assume that biomass production is proportional to the solar radiation absorbed by the stand canopy (after Monteith, 1977). The influence of environmental factors, such as temperature, soil water and nitrogen availability, on the efficiency with which the absorbed radiation is converted into biomass, is accounted for by using appropriated modifiers. The same approach was used in this thesis to model the growth of short rotation willow coppice (SRWC) forests in Southern Sweden.

The model presented n the thesis seeks to combine simplicity with robustness. It requires a limited amount of information as input, still it is looking for to mimic the most important process involved in carbon, water and nitrogen dynamics of willow forest systems. Further it is discussed what is gained (in applicability) by increasing model complexity to account for soil water and nitrogen conditions.

Objectives

The overall aim was to evaluate the relevance of modelling different processes for prediction of willow forests productivity under different site conditions. This aim was achieved in terms of four studies with the following aims:

to determine the radiation use efficiency of a willow stand growing under non-limiting conditions (paper I);

to test to which degree the growth of fertilised willow stands can be explained by the absorbed solar radiation and shoot mortality (paper II);

to determine to which extent the degree of explanation can be improved by considering the effect of soil water (paper III) and nitrogen (paper IV) availability on willow growth.

Methods

Estimation of the radiation use efficiency

Two approaches were used to estimate the radiation use efficiency of willows. First, the radiation use efficiency of a willow stand was determined in terms of energy conversion efficiency (ECE) with which the solar radiation energy reaching the stand, over the growing season, is converted into stem biomass (Paper I). ECE was calculated as the ratio between the energy in stem wood (E_{sw}) accumulated over the growing season (veg.), E_{sw} (MJ m^{-2} veg.$^{-1}$), and the energy of the received incoming solar radiation (E_{sr}) during the growing season, E_{sr} (MJ m^{-2} veg.$^{-1}$)

$$ECE=E_{sw}/E_{sr} \qquad\qquad (1)$$

In the second approach, the radiation use efficiency values (ε) were based on estimated absorbed radiation and calculated for different shoot ages (Paper II).

$$\varepsilon = \varepsilon_{Max}\, f(t_{Age}) \qquad\qquad (2)$$

where ε_{Max} is the maximum radiation use efficiency and $f(t_{Age})$ is the shoot age reduction factor. ε is the efficiency with which the stand utilises the absorbed radiation to produce new stem biomass.

The possible limitations on ε, due to shortage of water or N, are accounted for by the water reduction factor (f_W) (see Paper III) and the growth nitrogen response factor (f_N) (see Paper IV), respectively.

Modelling approach

The basic idea, followed in the studies presented in this thesis, was to construct a simplified process based (mechanistic) growth model for SRWC. To achieve this, empirical elements were integrated in the model at system level.

The starting point was to simulate the willow growth under unstressed conditions, i.e., as being mainly determined by atmospheric limitations on the photosynthesis processes, and intra-specific competition (RUE model, Paper II). However, as photosynthesis is also influenced by soill and management factors, other processes dealing with water balance (RUE-W model, Paper III) and nutrients (N) cycling (RUE-W-N, Paper IV) were simulated in order to increase model applicability.

Further the model has to be flexible to use. Depending on the intended use of the model, i.e., what should be predicted and which processes to include, the user should be able to select different degrees of complexity. To achieve this the model was constructed by three modules, each of them simulating the influence of the different main factors determining willow growth.

Those three modules are: 1) Biomass module, which simulates the influence of light (incoming solar radiation), shoot-age and mortality on willow growth (see Figure 1 in Paper II). 2) Water module, which simulates the soil water availability for plant growth taking into account the soil type (see Figure 1 in Paper III). 3) Nitrogen module, which simulates the soil nitrogen availability for plant growth taking into account the soil type and fertilisation regime (see Figure 1 in Paper IV). In the simulations, these modules can be linked and used together or separately. This allows for comparisons of the benefits, in terms of model predictability, of increasing model complexity to account for soil water and N conditions in different environmental situations. When only the biomass module is used in the simulations the model is named - RUE model -. If also the water module is used, then the model is named – RUE-W model -. If all three modules

are used then the model is called – RUE-W-N model -. Comparing the results obtained allows inferring which process are determinant to include in the simulations to get reasonable predictions in different circumstances.

Biomass production

In the RUE model (Paper I), willow stem biomass production ($\Delta W/\Delta t$), is simulated annually, as a function of the global radiation reaching the stand during the growing season (R_{sVeg}) and the fraction absorbed by the stand's canopy (α), radiation use efficiency (ε), shoot age (t_{Age}) and the fraction of biomass (W) lost by mortality (m).

$$\Delta W/\Delta t = R_{sVeg}\,\alpha(t_{Age})\,\varepsilon(t_{Age})\,(1\text{-}m) - m\,W_{tAge\text{-}1} - W_{Harvest} \qquad (3)$$

Both, the absorbed radiation and the radiation use efficiency, depend on shoot age (t_{Age}). At harvest stem biomass is removed ($W_{Harvest}$) from the system. Driving variables are daily sums of global radiation and daily means of air temperature. The temperature determines the start of the growing season. Further, initial values for biomass and harvest dates are needed as input.

Since commercial willow plantations, by norm, are not irrigated, and if fertilised the level of fertilisation may vary considerably, growth reduction factors were introduced to represent to which extent environmental conditions are sub-optimal.

In the RUE-W model (Paper III), stem biomass production depends also on the f_W, function that represents the possible limiting effect of soil water availability on willow growth. In the RUE-W-N model (Paper IV), the effect of nitrogen availability on stem biomass production is represented by the f_N.

The stem biomass production is then determined from

$$\Delta W/\Delta t = R_{sVeg}\,\alpha(t_{Age})\,\varepsilon(t_{Age})\,f_W\,f_N\,(1\text{-}m) - m\,W_{tAge\text{-}1} - W_{Harvest} \qquad (4)$$

At harvest, besides stem biomass ($W_{Harvest}$), also N is taken way from the system (see Paper IV).

Water availability

Water availability is simulated daily by the water module with basis on process for throughfall, infiltration, soil water storage, capillary rise, run off, evapotranspiration and root uptake (Paper III). Simulations are made similar to the water part of the SOIL (Jansson, 1991; Jansson & Halldin, 1979) and COUP (Jansson & Karlberg, 2001) models. However, the structure, in terms of number of soil layers (three layers) and processes considered, is simplified to facilitate parameterisation when applying the model to field data. Water dynamics is simulated in the vertical dimension and horizontal water flows and soil heat are not considered. (Paper III).

The daily simulated water availability is used to estimate an annual value of f_W. Low water availability is expressed as the reduction of annual transpiration (ΣE_t) relative to the annual potential transpiration (ΣE_{tp}).

$$f_W = a_W \left(1 - (\Sigma E_{tp} - \Sigma E_t) / \Sigma E_{tp}\right) \qquad\qquad 0 \leq f_W \leq 1 \qquad (5)$$

The coefficient a_W is larger than one, which makes growth not sensitive to transpiration reductions close to potential transpiration rates.

The water module is dependent on the biomass simulations on an annual basis, by means of the standing stem biomass at start of the growing season, that determines the leaf area and root depth development during the coming season, which are input to the water module (Paper III). Other inputs needed (beyond the ones needed for biomass simulations) are daily data on rainfall, air humidity, wind speed and irrigation, and USDA soil type.

Nitrogen availability

Nitrogen availability simulations are based on processes for root N uptake, decomposition of dead organic matter, mineralisation or immobilisation of N, nitrification and nitrate transport (Paper IV). Simulations are, to a large extent, made similar to the SOILN model (Eckersten et al. 1998; Johnson et al. 1987), but the structure is simplified as concerns the number of soil layers represented. Only three soil layers are included (Paper IV).

Nitrogen deficit ($N_{Deficit}$) is expressed as low nitrogen availability in relation to plant N demand (ΣN_{Dem}), and is used to reduce annual growth in terms of the reduction factor f_N.

$$f_N = 1 - b_N \, N_{Deficit} / (a_N \, \Sigma N_{Dem}) \qquad\qquad 0 \leq f_N \leq 1 \qquad (6)$$

The parameter a_N (= 0.7) is the fraction of maximal plant demand for N uptake that is needed for maximal growth rate. The parameter b_N (= 0.8) is the relative decrease of f_N caused by an increased N deficit.

The N deficit is the difference between plant N demand for maximal growth (a_N ΣN_{Dem}) and N availability. The N availability is the sum of annual net mineralisation, deposition, fertilisation and soil mineral N at the beginning of the year, plus the internal supply of N from the plant itself, minus annual losses (via leaching and denitrification). The annual sums are calculated from simulated daily values.

The nitrogen module needs input of daily values on plant N demand and litter formation. These are derived from the leaf area, which in turn is estimated from the standing stem biomass (see water module above). Also the soil water content, the relative soil water content and water flows between layers, as simulated by the water model, are daily input to the nitrogen module. Further, it needs management data on fertilisation.

Calibration site

Model calibrations were conducted with data from a willow stand (Modellskogen) growing on a clay soil in Uppsala. The data comprise the annual stem biomass production over 10 years (three cutting cycles). The stand was both fertilised (ca. 105 kg N ha^{-1} y^{-1}) and irrigated (ca. 100 mm y^{-1}). A summarised description of the site and plantation characteristics is given in Appendix (Tables A1).

Data, from the fertilisation trial at the site Korrvike, were used to calibrate the response of the nitrogen growth factor to nitrogen availability. The trial comprises four fertilisation levels with average N supplies of: zero (0); 55 kg N ha^{-1} y^{-1}; 110 kg N ha^{-1} y^{-1} and 160 kg N ha^{-1} y^{-1} (Tables A1 and A2).

Test sites

Data from 22 willow coppice stands, located at five different sites in southern Sweden, were used to assess the ability of the model to reproduce the variations in stem biomass production (Tables A1 and A2 in Appendix). The data comprise annual biomass production over two to nine years (one or two cutting cycles). The fertilisation level between stands varied from 0 to 160 kg N ha^{-1} y^{-1} and none of the test stands was watered. The stands were constituted by clone mixtures (except the four stands at the site Korrvike). According to USDA classification four soil types, clay, clay loam, sandy loam and loamy sand, are represented. All simulations were performed using daily weather data from the nearest climate station (Table A1 and A2 in Appendix) in the national weather service's network stations.

In the papers included in this thesis, model performance was evaluated by using several statistical measures. Here, in the summary, model predictability and comparisons of model performance are presented and discussed with basis on the coefficient of determination (R^2) of the regression line between simulated and measured values. Model predictability is compared for three groups of test data: 1) **All** – includes all the 22 test stands; 2) **Fertilised** – includes the 12 stands that, on average, received more than 75 kg N ha^{-1} y^{-1} (<u>High and Moderate fertilisation in Table A1</u>); and 3) **Unfertilised** - includes the 10 stands that, on average, received less than 65 kg N ha^{-1} y^{-1} (<u>Low and No fertilisation in Table A2</u>).

In all stands the annual measurements of standing stem biomass were done during winter and non- destructively. Five of the test stands had a bad establishment and produced less than 2.5 t ha^{-1} during the first year after plantation. For these stands the simulation start was delayed by one year: the age of the shoots growing during the second growing season after plantation was set equal to shoot age one and the first growing season was set to be the plantation year.

Results

Radiation use efficiency

The radiation use efficiency, of the Modellskogen stand, both based on incoming global radiation (Paper I) and on absorbed radiation (Paper II), varies with shoot age (Table 1). Efficiency values, based on global radiation, are lower for shoot ages I and IV than for shoot ages II and III. Efficiency values, based on absorbed radiation decrease from shoot age II.

Table 1- *Radiation use efficiency values (ε), for each shoot age, calculated and estimated for the Modellskogen forest. Also presented are average stem biomass produced and the fraction of absorbed radiation (α) for each shoot age. All the values are accounted for the growing season period.*

Shoot age	Biomass (g m^{-2})	ε based on global radiation (g MJ^{-1})		ε based on absorbed radiation (g MJ^{-1})	α
		Calculated	ε * α (calibrated)	Calibrated	Determined
I	631	0.32	0.38	0.64	0.59
II	1219	0.55	0.66	0.91	0.73
III	1072	0.46	0.61	0.73	0.76
IV	717	0.33	0.45	0.61	0.74

The difference between calculated and calibrated ε values, based on total radiation, results from the fact that the calculated values also include effects of shoot mortality. In the model the losses of biomass due to shoot mortality are explicitly calculated and are not a part of the ε values.

Simulations of biomass production with the RUE model

The purpose of the first model – RUE model – (presented in Paper II) was to investigate the reliability of a model based on the radiation-use-efficiency concept to mimic the growth of well fertilised (> 75 kg N ha^{-1} y^{-1}) willow coppice stands, growing at different locations in southern Sweden.

To account for the influence of the high plant densities and the short harvest cycles (3 to 5 years) characteristics of the willow coppice systems, shoot-age and shoot mortality due to self-thinning are explicitly included in model simulations. It was assumed that mortality implies direct losses of biomass produced and shoot age has a direct effect on the fraction of solar radiation that is absorbed and on the radiation use efficiency.

The RUE model was tested on 12 (fertilised but not irrigated) stands and it was able to explain 82% of the observed variations in biomass production at harvest. If applied only to the six stands with a similar level of fertilisation as the Modellskogen the degree of explanation increased to 90%. However, the RUE model's ability to reproduce variations on the annual biomass production was low.

Only ca. 50% of the annual variations were explained by the model. This suggests that the growth of particular years might be significantly influenced by factors not accounted for in the model (for example drought or nutrient deficits).

Simulations of biomass production with the RUE-W model

The results above show that a model based on the radiation-use-efficiency concept can be appropriated to simulate willow biomass production at harvest. However, theoretically the use of the RUE model is constrained to unstressed stands. The purpose of the second model – RUE-W model – (Paper III) is therefore, to find to what extent, incorporating the variability in water conditions between sites and years, contributes to explain variations on willow biomass production.

All the assumptions made in the previous study were kept except that now the effect of sub-optimal soil water conditions on willow growth (i.e., on willow biomass production) are explicitly represented in terms of a water reduction factor.

The RUE-W model was tested on the same 12 stands as the RUE model and it was able to explain 76% of the variations in biomass production at harvest and 27% of the variations in annual production. The results show that considering the effects of soil water availability on willow growth do not improved biomass prediction compared to considering the effects of absorbed radiation, shoot age and mortality alone. However, one exception was found for the third year's production where the R^2 increased from the 0.28 obtained with the RUE model to 0.44 obtained with the RUE-W model. Further, from the sensitivity test on how growth is affected by a reduction of precipitation rate for different soil types (see Figure 7, Paper III), the RUE-W model response to differences in water supply seems to be realistic.

Simulations of biomass production with the RUE-W-N model

In the previous model the ability of different type of soils to supply water to the plants was simulated for fertilised stands. These are not, however, the norm among private-owned willow coppice stands. The purpose of the third model – RUE-W-N model – (Paper IV) was to determine, to what extent, including the variations in soil N availability between sites and fertilisation regimes, can contribute to explain the variations in willow biomass production observed at different sites and fertilisation levels.

Nitrogen limitations to growth are expressed as low nitrogen availability in relation to plant demand and are explicitly represented in terms of a nitrogen reduction factor. All the other assumptions were the same as in the previous study.

The RUE-W-N model was tested on all the 22 test stands. However, the results presented here bellow refer to only 18 stands (10 Fertilised and 8 Unfertilised), as the results from the stands at the site Grimstad were not included as this site was located bellow an esker (Alriksson, 1997) and water conditions were not possible to predict with our model approach. The model was able to explain 82 to 86% of

the observed variations in yield at harvest and 32 to 41% of the variations in annual biomass production (Table 2). At harvest, model predictability is higher for Unfertilised stands ($R^2 = 0.86$), while the best predictions of annual biomass production are obtained for All stands ($R^2 = 0.41$).

Model comparisons

In order to investigate, in which conditions, the inclusion of processes to simulate soil water and nitrogen availability leads to increased model predictability, the RUE and the RUE-W were also tested on all (18) stands.

The degree of explanation of variation in biomass production at harvest was high for all models (Table 2). In contrast, for variations in annual production, the degree of explanation was low for all models (Table2). Regarding variations in productivity for each shoot-age, they tend to be better explained for one-year-old shoots than for two- or three-years-old shoots (Table 2).

The results show that, the processes included on the RUE model satisfactorily described variations in biomass production at harvest, for stands with a similar level of fertilisation. The inclusion of processes to simulate water and nitrogen availability, on different types of soils, could not explain more than another 2% of the variation observed for Unfertilised stands (R^2 improved from 0.84 with the RUE model to 0.86 with the RUE-W-N model, Table 2). For Fertilised stands the inclusion of such processes even influenced predictability negatively. This results suggest that variations in harvest production, of willow stands with similar N supply, can be estimated by a simple model such as RUE that only requires climate data that are routinely recorded in weather stations.

However, when model predictability is compared, regarding variations in biomass production at harvest, for All stands, improvements, arising from taking into account variations in the soil ability to supply plants with water and nitrogen become apparent. For All stands, model predictability increased from $R^2 = 0.70$ with the RUE model to $R^2 = 0.82$ with the RUE-W-N model (Table 2). This indicates that, model predictability benefits from the inclusion, of the effect of simulated soil water and nitrogen availability on willow growth, when simulating stands that are growing under different N supply regimes.

Predictions of the variations in annual biomass production follow the same pattern as predictions of variations in production at harvest. For Unfertilised and Fertilised stands, model predictability does not benefit from increased complexity to account for water and nitrogen availability in the soil, while predictability for All stands is improved if soil and nitrogen availability are considered in the simulations.

Including solely soil water availability (RUE-W model) had a negative effect on model predictability except for biomass production of three-years-old shoots (Year 3, Table 2). In fact, variations in biomass production of three-years-old shoots, are considerably better explained when soil water availability (for All and Fertilised

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stands), or both soil water and nitrogen availability (for Unfertilised stands), are considered than if only the effects of radiation absorbed, shoot age and mortality are accounted for.

Discussion

Radiation use efficiency

The results presented here show that radiation use efficiency, of willow plants, is not constant but varies with shoot age within a cutting cycle of four years (Table 1). If efficiency is based on global radiation (Paper I) the lowest values are found for shoot ages I and IV. When calculated this way, the radiation use efficiency accounts implicitly for both absorbed radiation and shoot mortality. Therefore, the lower efficiency values for the youngest shoots, might be a result of a delay in canopy closure (Paper I). This in turn is due to a delay in leaf area development as the older shoots have an earlier and faster canopy closure (Eckersten & Nilsson, 1990). For the oldest shoots, the lower efficiency values, might be a consequence of loss of biomass due to shoot mortality caused by self-thinning (Paper I). Mortality studies on the Modellskogen stand showed that mortality occurs among the smallest individuals, which is consistent with a situation of self-thinning ongoing in the stand (Verwijst, 1991; Verwijst, 1996).

If efficiency (ε) is based on absorbed radiation (Paper II), efficiency decreases with shoot age from shoot age II. When this approach is used, the radiation absorption and shoot mortality are explicitly estimated and not a part of the efficiency values. Leaf area development seems to be more important for stem biomass production than ε. Despite the low production of the one-year-old shoots, ε was relatively high, which might be explained by the low fraction of absorbed radiation This in turn results from the longer time needed for young shoots to develop a closed canopy. Cannell (1988) based on values of light use efficiency and light interception, determined for irrigated and fertilised stands, concluded that an early leaf expansion was more significant for biomass production than the efficiency in using the absorbed radiation. Also Lawlor (1995), on a study of photosynthesis, refers that reduced "light conversion efficiency have smaller effects on production" than a poor leaf area development

Table 5: *Coefficient of determination (R^2) values of the regression lines between observed and simulated values obtained with the different models. The n is the number of data points used in the regression analysis. Figures in bold denotes the model that gives the highest R^2 value for each situation.*

Stands	Model	Harvest	Annual (all years)	Year 1	Year 2	Year 3
All	RUE	R2 = 0.70; n=19	R2 = 0.38; n=51	**R2 = 0.72; n=20**	R2 = 0.14; n=20	R2 = 0.00; n=10
	RUE-W	R2 = 0.69; n=19	R2 = 0.20; n=51	R2 = 0.68; n=20	R2 = 0.01; n=20	**R2 = 0.47; n=10**
	RUE-W-N	**R2 = 0.82; n=19**	**R2 = 0.41; n=51**	R2 = 0.63; n=20	**R2 = 0.38; n=20**	R2 = 0.21; n=10
Fert.	RUE	**R2 = 0.85; n=11**	**R2 = 0.48; n=31**	**R2 = 0.74; n=12**	**R2 = 0.04; n=12**	R2 = 0.09; n=6
	RUE-W	R2 = 0.77; n=11	R2 = 0.34; n=31	R2 = 0.68; n=12	R2 = 0.00; n=12	**R2 = 0.77; n=6**
	RUE-W-N	R2 = 0.83; n=11	R2 = 0.40; n=31	R2 = 0.52; n=12	R2 = 0.01; n=12	R2 = 0.61; n=6
Unfert.	RUE	R2 = 0.84; n=8	**R2 = 0.32; n=20**	R2 = 0.76; n=8	**R2 = 0.49; n=8**	R2 = 0.31; n=4
	RUE-W	R2 = 0.83; n=8	R2 = 0.08; n=20	R2 = 0.76; n=8	R2 = 0.08; n=8	R2 = 0.31; n=4
	RUE-W-N	**R2 = 0.86; n=8**	**R2 = 0.32; n=20**	**R2 = 0.80; n=8**	R2 = 0.28; n=8	**R2 = 0.74; n=4**

If efficiency is based on absorbed radiation (as in Paper II), efficiency decreases with shoot age from shoot age II. When this approach is used, the radiation absorption and shoot mortality are explicitly estimated and not a part of the efficiency values. Leaf area development seems to be more important for stem biomass production than ε. Despite the relatively high ε of the one-year-old shoots, their biomass production was the lowest, which might be explained by their low fraction of absorbed radiation This in turn results from the longer time needed for young shoots to develop a closed canopy. Cannell (1987) based on values of light use efficiency and light interception, determined for irrigated and fertilised stands, concluded that an early leaf expansion was more significant for biomass production than the efficiency in using the absorbed radiation. Also Lawlor (1995), on a study of photosynthesis, refers that reduced "light conversion efficiency have smaller effects on production" than a poor leaf area development

The differences in efficiency between the years might reflect changes in partition of assimilates and assimilates being used for other purposes (for example respiration) than stem biomass production. However this is not further investigated within the scope of the studies presented here.

Model comparisons

By following the modelling strategy described above, productivity assessments, for willow coppice forests, were made based on radiation absorption and conversion into biomass, shoot age and mortality, including, as a choice, the effects of water and nitrogen stress on willow growth. The benefits, of accounting for soil water and nitrogen conditions were evaluated for predictions of variation in productivity between sites, years and fertilisation level. In this respect, this is a pioneer study for willow coppice systems.

As for other trees stands, for example *Eucalyptus globulus* (Landsberg & Hingston, 1996; Battaglia, Sands & Candy, 1999), the variations in productivity, at harvest, of willow coppice stands can be reasonably described by a model that integrates mechanistic and empirical elements at system level. Further, this study indicates that most of those variations can be simulated using a simple mechanistic model based on radiation-use efficiency, and that the inclusion of process to simulate soil water and nitrogen conditions, in general, conveys little extra improvements on model predictability.

It is not uncommon that more complex models do not show more precise results than simpler ones (Wegehenkel, 2000). This is a result of the trade-off between increased explanatory power, due to the new process introduced, and increased prediction uncertainty due to introduction of new sources of error into model simulations (Håkanson, 1995; Fortin & Moon, 1999).

Another general trend is that model predictions are better for biomass production at harvest than for annual biomass production. This may result from the fact that non-linearities, in the growth response to environmental factors, tend to be less

apparent over time (Landsberg & Hingston, 1996). For particular years, the effect of singular events (e.g. frost, browsing), on willow production, might be significant, but levelled out when considering production over the whole cutting cycle. It should be noted, however, that with the exception of the first year, the simulated biomass production depends on the simulated value of the previous year. This allows for propagation of errors, for example, if production one year is underestimated, in the next year mortality will be underestimated and production overestimated. However, as concerns the accumulated growth over years the error tends to be levelled out.

Variations in productivity at harvest, of the willow coppice stands used, simulated by the RUE model are better estimated for stands with a similar fertilisation level (Table 2). Further, the best estimates, with the RUE model, are obtained for the six stands with a fertilisation level close to the level applied to the calibration stand Modellskogen ($R^2 = 0.90$; see Paper II). This indicates that the RUE model is more appropriated to simulate biomass production of stands receiving a similar N supply, which is coherent since the RUE model does not account for the effect, on growth, of variations in soil nitrogen availability. It also indicates that the fertilisation level (i.e., N availability) influences willow production. Nevertheless, the high predictability of the RUE model, indicates that willow production, of the stands considered, is most dependent on the absorbed radiation, shoot age and mortality.

The inclusion of simulations of soil water availability (RUE-W model) only had a positive effect, on model predictability, in the third year (Table 2). Overall, model predictability was not improved despite reasonable estimates of the influence of a reduction in water supply on growth (see Paper III). This might be due to problems in having proper input data or / and due to plant adaptation to dryer environments.

First, roots may grow deeper, than it was assumed by the model, and thereby lead to an inaccurate estimation of the amount of water available for root uptake and of the actual evapotranspiration (Boonyatharokul & Walker, 1979). The occurrence and efficiency of deep roots has been found to be of major importance for estimate evapotranspiration on a willow stand (Persson & Jansson, 1989). Also, for example, for eucalyptus (Landsberg & Hingston, 1996) and olive trees (Palomo et al., 2002), low or no effects of water, on tree growth, were related to a large root depth.

Second, roots might grow preferentially along fissures in the soil, as have been found for poplar coppice stands (Hall et al., 1998), this alter the value of the "so-called macroporosity and produce preferential direction for water movement (Laio et al., 2001). In this case, soil moisture might be misleading in representing water availability.

In addition, the RUE-W model was calibrated against an irrigated willow stand, however, it is possible that plant water demand for growth is lower in the non-irrigated willow stands used to test the model. Many plants possess adaptations

that increase their tolerance to drought (c.f. Kramer, 1983). For example, growing in dryer environments they might increase their water use efficiency.

So it is possible that, the growth of the simulated willow stands has not been significantly limited by water shortage. In this case model performance does not benefits from the inclusion of explicit simulations of water availability. The benefits are masked by that new source for errors were introduced.

The inclusion of simulations of soil water and nitrogen availability (RUE-W-N model), in general, improved model predictability, for **Unfertilised** and for **All** stands (Table 2). For **Fertilised** stands, on contrary, the predictability is slightly decreased, except for the third year (Table 2). This might be due to the fact that, for these stands, limitations on growth, due to N deficits, are small. In these circumstances, as referred for water availability, model performance does not benefit from the inclusion of explicit simulations of N availability.

For **Unfertilised** stands the improvements obtained are, however, very small. If the RUE-W-N model correctly simulates N availability, and its effect on growth, this indicates that the observed variations in productivity, of these stands, were poorly related to variations in the soils natural N availability. Results from simulations, of the behaviour of the growth factor (f_N), under different fertilisation and soil type scenarios, showed a similar response as obtained, from experimental results, by Weih & Nordh (2002) and Aronsson & Bergström (2001) (see further Paper IV).

Could it be that simulations of N availability are not realistic? Simulated mineralisation rates and N leaching are similar to those estimated for agricultural soils by Kätterer et al. (1999). However, short-term dynamics of N leaching was poorly simulated (see Paper IV). This might have introduced an error, although not very large, in the estimated N availability.

For **All** stands, the benefits, on model predictability, of including explicit simulations of soil water and availability, are more evident, especially for production at harvest. This, in connection with the results obtained for **Unfertilised** stands, indicate that the fertilisation level is more valuable to describe the variations in biomass production, of the willow test stands, than the ability of the different soil types to supply N to plant growth.

When comparing the results from this study with the results from other studies on the evaluation of the effects of different environmental or management factors on willow growth, there are both similar (Tahvanainen & Rytkönen, 1999) and contradictory results (Alriksson, 1997). Tahvanainen & Rytkönen (1999) found that climatic conditions had a stronger influence, on willow biomass production, than soil properties. While Alriksson (1997) found that willow productivity had a stronger relationship to soil texture and speculate that site properties, related to clay content, might be more important than N-fertilisation.

One possible explanation for these discrepant results might be the time perspective. The results presented by (Alriksson, 1997) are from the fifth and sixth growing season, while the results presented by Tahvanainen & Rytkönen (1999), as well as the results presented here, are based on biomass production after three growing seasons. It might be that, the influence of soil properties on N availability for plant growth might not be high enough to produce significant variations in willow productivity during the first years, compared to the influence of climatic factors or fertilisation. This idea is supported by the fact that better estimates are obtained, both by RUE-W and RUE-W-N models, for the third year than if RUE alone is used, indicating that soil related factors might become more important with time. However, the number of simulated third years was rather small (n=4) and the model needed further testing.

Overall, the effect was small, probably because we couldn't test the modified models against growth data from a wide range of environments. The test data did not included years with severe water stress and the sites chosen for the used plantations were from former agricultural land (i.e., fertile soils). Reductions in soil nitrogen may develop over longer periods of time. Two other factors that also might contribute to decrease differences in N availability between sites are an increased allocation of growth to roots on poor N environments (Cannel & Dewar, 1994) and an increased uptake by mycorrhiza on the N poor sites (Wallander, 1995). An increased allocation to roots due to poor N status would increase the N availability for the willow stands on the poor sites.

Finally, I would like to mention that, all the test stands, with exception of the stands at Korrvike, were constituted of a mixture of clones and differences, between willow clones, in response to water and N stress have been shown (see Weih 2001). Therefore, it is possible that the genetic variation of the willow clones, in response to water and nitrogen stress, counteracts the differences in water and N supply by the different soil types.

Conclusions

- Radiation use efficiency of willow plants varies with shoot age.

- In southern Sweden, the variations in harvest yield of willow stands, growing on different types of soils on former arable land, can satisfactorily be simulated by a model based on canopy intercepted solar radiation, shoot mortality and shoot age.

- Accounting for differences in water conditions between soil types does not improve model predictability of growth.

- Accounting for differences both in soil water and nitrogen supply, improves model predictability only for stands growing under different fertilisation levels.

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- For stands with a similar fertilisation level, water and nitrogen simulations do not improve model predictability, compared to account for radiation absorbed, shoot age and shoot mortality, alone.

- The level of fertilisation seems to be more important than the capacity of the different soils to deliver N, for predicting willow growth.

- Variations in biomass production from year to year are indicated to be poorly related to annual variations in solar radiation, shoot mortality or soil water and nitrogen availability. This conclusion is, however, tentative since the simulations not used the measured values of biomass at the beginning of the season instead of the simulated values.

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Acknowledgements

Appendix A

The following tables show information for site and plantation characteristics of the stands used and are common for Paper II, III and IV.

Table A1. *Summary of the site and plantation characteristics for the high fertilised test and calibration sites at Uppsala ("modellskogen"). No stand was watered, except Modellskogen. Harvest is made in winter.*

Site	Field	Management	Soil	Size and density of plantation	Plantation year and harvest	Source
Uppsala	Modellskogen	1985-1992 the stand received 50 to 300 kg N ha^{-1} y^{-1} and 50 to 400 mm water. 1993 and 1994 was not fertilised or watered.	Clay	2.7 ha; 20.4*10^3 cuttings ha^{-1}.	Planted 1984. Harvested winters 1986/87, 1990/91 & 1994/95.	Verwijst, (1996)
	Gottsunda	Fertilised with 70 to 140 kg N ha^{-1} y^{-1}.	Clay loam	0.69 ha; 20*10^3 cuttings ha^{-1}	Planted 1994. Harvested winter 1997/98	Personal comm. Nils-Erik North
Västerås	Brunnby	Fertilised with 50 to 120 kg N ha^{-1} y^{-1}. No fertilisation the years 1997 and 1998.	Clay	0.52 ha; 20*10^3 cuttings ha^{-1}	Planted 1990. Harvested winters 1993/94 & 1997/98	
	Korrvike C	Fertilised with 90 to 150 kg N ha^{-1} y^{-1}		896 m^2; 2 cuttings m^{-2}	Planted 1989. Harvested winter 1992/93	
	Korrvike D	Fertilised with 150 to 180 kg N ha^{-1} y^{-1}				
	Bännebo C	Fertilised with 90 to 150 kg N ha^{-1} y^{-1}.		156 m^2; 2 cuttings m^{-2}	Planted 1989. Harvested winter 1992/93	
	Bännebo D	Fertilised with 150 to 180 kg N ha^{-1} y^{-1}				
Vingåker	Grimstad C	Fertilised with 90 to 150 kg N ha^{-1} y^{-1}	Loamy sand	780 m^2; 2 cuttings m^{-2}	Planted 1989. Harvested winter 1992/93	Alriksson, (1997)
	Grimstad D	Fertilised with 150 to 180 kg N ha^{-1} y^{-1}				
Malmslätt	Logården C	Fertilised with 90 to 150 kg N ha^{-1} y^{-1}.	Clay loam	780 m^2; 2 cuttings m^{-2}	Planted 1988 Harvested winter 1991/92	
	Logården D	Fertilised with 150 to 180 kg N ha^{-1} y^{-1}.				
Lund	Borgeby C	Fertilised with 90 to 150 kg N ha^{-1} y^{-1}.	Sandy loam	780 m^2; 2 cuttings m^{-2}	Planted 1989. Harvested winter 1992/93	
	Borgeby D	Fertilised with 150 to 180 kg N ha^{-1} y^{-1}.				

Table A2. *Summary of the site and plantation characteristics for the non and low fertilised test. No stand was watered. Harvest is made in winter.*

Site	Field	Management	Soil	Size and density of plantation	Plantation year and harvest	Source
Västerås	Korrvike A	No fertilisation	Clay	896 m^2; 2 cuttings m^{-2}	Planted 1989. Harvested winter 1992/93	
	Korrvike B	Fertilised with 45 to 75 kg N ha^{-1} y^{-1}				
	Bännebo A	No fertilisation		156 m^2; 2 cuttings m^{-2}	Planted 1989. Harvested winter 1992/93	
	Bännebo B	Fertilised with 45 to 75 kg N ha^{-1} y^{-1}				
Vingåker	Grimstad A	No fertilisation	Loamy sand	780 m^2; 2 cuttings m^{-2}	Planted 1989. Harvested winter 1992/93	Alriksson, (1997)
	Grimstad B	Fertilised with 45 to 75 kg N ha^{-1} y^{-1}				
Malmslätt	Logården A	No fertilisation	Clay loam	780 m^2; 2 cuttings m^{-2}	Planted 1988 Harvested winter 1991/92	
	Logården B	Fertilised with 45 to 75 kg N ha^{-1} y^{-1}				
Lund	Borgeby A	No fertilisation	Sandy loam	780 m^2; 2 cuttings m^{-2}	Planted 1989. Harvested winter 1992/93	
	Borgeby B	Fertilised with 45 to 75 kg N ha^{-1} y^{-1}				