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Estimation of Above-Ground Biomass of Wetlands

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1. Introduction

Despite global importance of wetlands, estimations of their production and biomass have received little attention (Campbell et al., 2000). This chapter concentrates on analysis of the composition and above-ground biomass of floodplain grasslands and fen vegetation in the Northern forest zone. Both vegetation types were extensively used for hay and/or grazing up to the middle of the 20th century, and abandoned later.

Systematic biomass estimations were conducted in the 1970s–1980s (Estonian data from 1977–1980; most data from Canada from 1972–1978 (Campbell et al., 2000)) when they were feasible for agricultural use. Papers on vegetation production and above-ground biomass of wetlands are quite scarce nowadays. Biomass has sometimes been measured for developing community structure theories, e.g. Zobel & Liira (1997) included some wet grasslands into analysis of richness vs biomass relationship. Still, some thorough reviews can be found like an overview of biomass of rich fen types in South England and Wales by Wheeler & Shaw (1991). New interest in the subject has risen in the context of biomass use for bioenergy production (e.g. Rösch et al., 2009).

Many plant species cannot survive without special accommodation to wetland conditions. The composition of wetland vegetation is mostly controlled by the wetland water level (WL) (Bootsma & Wassen, 1996; Hájková et al., 2004; Barry et al., 2008). Wilcox & Nichols (2008) and Ilomets et al. (2010) found that the diversity and habitat value of plant communities depend on the wetland WL and the water level amplitude between dry and wet seasons (WLA). In fens with a constantly high WL rhizome-spreading graminoids and herbs dominate, while drainage and fluctuating WL support high tussock-forming graminoids.

A specific feature of both floodplain grassland and fen vegetation is high patchiness due to variations in WL and WLA caused by microtopography (Liira et al., 2009). Tussocks, formed by herbaceous plants or tree stumps, locally increase the habitat variability even more (Liira et al., 2009; Ilomets et al., 2010).

Total biomass of wetland vegetation is significantly affected by three main factors: the N:P ratio, total nutrient supply and morphological and physiological traits of plants (Güsewell, 2005). Biomass variations are higher on moister sites such as wet floodplain grasslands (Truus & Puusild, 2009) and fens (Ilomets et al., 2010). The height and coverage of tussocks increases with denser or deeper drainage. About 52% of the vascular plant species variance occurs due to four environmental variables: amplitude of WL (between spring flooding and midsummer dry period), midsummer WL, mire water pH and electrical conductivity (Ilomets et al., 2010).

Truus & Puusild (2009) found strong relation of the above-ground biomass with the management regime but not with the variations in site conditions on wet and moist floodplain grasslands. Wilson & Keddy (1986), Moore & Keddy (1989) and Garica et al. (1993) detected general hump-back relationship between species richness and biomass, but it has also been shown that a high number of factors can complicate prediction of species richness from community biomass (Gough et al., 1994).

2. Factors affecting wetland productivity and species richness

2.1 Relationship between species richness and biomass

The relation between plant species richness and biomass was first discussed by Grime (1973, 1979) and Al-Mufti et al. (1977) when describing general hump-back relationship between species density and community biomass. According to these authors, maximum species richness can be found at medium values of biomass. Later, this relation has been approved (Wheeler & Giller, 1982) or denied (Gough et al., 1994). In the development of this theory Zobel & Liira (1997) attributed species richness to the plant ramet density.

Gough et al. (1994) established correlation between environmental conditions and species richness but not between biomass and environmental conditions. Therefore, the influence of environmental conditions on species richness could not be assumed strictly from biomass. Wheeler & Giller (1982), Boyer & Wheeler (1989) and Wheeler & Shaw (1991) recorded differences in biomass– species richness relation between community types (low-sedge low-productive fen, productive tall-sedge and reed fen, and fertile site communities with strong domination of *Filipendula ulmaria* or *Molinia cerulea*).

According to Gough et al. (1994), two types of processes operate in the species richness–productivity relation on wetlands:

- At low levels of productivity, species richness is primarily limited by the ability of the species to survive the abiotic conditions. In this range increase in productivity reflects a decrease in the harshness of the environment.
- At higher levels of community productivity, the decline in richness is believed to be related in some way to a greater degree of competitive exclusion with increasing productivity. For wetlands this relation was revealed by Wheeler & Giller (1982). Examining herbaceous fen vegetation, they found that species richness was negatively correlated to above-ground biomass.

Wet meadows are poorer in species than those on mineral soil. Two reasons could be pointed out:

- Hard environmental stress that excludes several plant species.
- The absence of management leading to domination of tall plants and accumulation of dead biomass on soil surface (Truus, 1998).

Strong correlation has been found in fens between the height and coverage of the tussock-forming graminoid *Molinia cerulea* in fens with fluctuating WL and midsummer WL minimum (Ilomets et al., 2010).

In general, relationship of species richness and above-ground biomass is complex and hardly predictable, especially for wetlands.

2.2 Limitations of productivity

2.2.1 Flood, water level and water level amplitude

On **floodplain meadows** the duration and intensivity of flooding serve as environmental determinants of plant species selection. Riverine floodwater pulses provide water, nutrient-rich material and sediments to floodplain wetlands, but flood pulses also act as a natural disturbance by removing biomass, scouring sediments and delivering turbid waters (Bayley & Guimond, 2009). Riparian ecosystems are among the most diverse systems on the world's continents (Nilsson et al., 1997). The intensity of natural processes taking place on floodplains is variable, depending on the properties of the river and shore. Estonian rivers are usually small and floodplains narrow. Thereby most riverborn nutrients settle on the 50 m wide belt close to the river channel[1] where productive high-growing vegetation develops. An exception is South Estonia where luxorious sandy sediments form rapidly desiccating low-productivity dry floodplain meadows.

The species composition of spring fen communities is mainly influenced by groundwater chemistry, especially pH, electrical conductivity and mineral richness (Hájek et al., 2002). It is unknown whether these factors affect species richness and the amount of above-ground biomass (Hájkova & Hájek, 2003).

2.2.2 Water and soil chemistry and nutrient availability

Water and soil chemistry and nutrient availability to plants are among the important factors controlling the diversity of wetland vegetation.

Floods bring extra nutrients to floodplain grasslands. Thus there is no N and P deficit and vegetation is luxorious. Management of grasslands removes nutrients from soil and biomass production decreases. Without management, however, annual biomass production increases.

Fens are characterized by high concentrations of cations in soil and water. The concentration of Ca, Fe, N, P and K in plants varies along the poor–rich fen vegetation gradient from poor *Sphagnum*-fens to calcareous fens, and from sedge-moss fens to forb-rich wet meadows (Rozbrojová & Hájek, 2008). The same study showed that the fertility gradient was largely independent of the poor–rich (pH/calcium) gradient. Nutrient limitations of fens are complicated: species in one community can have different limitations (Rozbrojová & Hájek, 2008). Low-productivity fen communities that support more rare species (Wassen et al., 2005) are rather P- or K- (co)limited, or limited by different environmental conditions (Rozbrojová & Hájek, 2008).

2.2.3 Management

Due to nutrient supply by floodwater, the soil of floodplain meadows is rich in nutrients and biomass productivity is high. The amounts of nutrients brought by floods is comparable to quantities taken away with the harvest or/and cattle grazing. Clipping increase species richness and shoot density but decrease above-ground biomass, thus creating more favourable conditions for more plant species. Bakker (2007) demonstrated that cutting reduces the vigour of tall competitive species, allowing smaller species coexist. Nowadays most of the floodplain meadows are left unmanaged. Hay is mown only in restricted areas for the purposes of environmental protection.

In comparison with other meadow types above-ground biomass production is lower on dry floodplain meadows and higher on floodplain marshes. Productivity is variable in all floodplain meadow community types depending on species composition (Table 1). On wet meadows the site moisture conditions are greatly responsible for plant ecological traits. On

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[1] Pork, K. (1984). Jõeluhtade looduslikus seisundis säilitamisest. In: *Looduskaitse ja põllumajandus.* Kumari, E., Randalu, I. & Hang, V. (Eds.). Academy of Sciences of the E.S.S.R, 58–70. [In Estonian]

permanently wet sites both tussock-forming and mat-forming graminoids dominate while herbs dominate where soil WL drops down at least in summer (Fig. 1). Comparison of Estonian data from the period of regular management (Table 1) with the period of abandonment (Tables 2 and 3) showed that productivity had risen due to accumulation of plant nutrients on unmanaged meadow soils. Above-ground biomass varied threefold, depending on the management regime (Table 3). Liira et al. (2009) also noticed that management lowered canopy height but revealed differences in functional trait structure in more detail.

Falinska (1991, 1995) described two stages in the after-abandonment vegetation succession in *Cirsium rivularis* phytocoenosis on wet grassland. The initial stage of the succession lasted about 9 years: half of 142 plant species retreated but 12 species became dominant and a macroforb meadow community (*Lysimachio vulgaris–Filipenduletum*) meadow with mosaic structure, including species like *Filipendula ulmaria, Carex cespitosa, C. acutiformis, Lythrum salicari*a and *Lysimachia vulgaris*, was formed. During the following 15 years a specific spatial complex developed, consisting of meadow and herbaceous communities and willow shrub aggregations with the first tree species. Next the *Circaeo-Alnetum* woodland community appeared. The succession exhibits differentiation of the horizontal structure – increase in patchiness, and differentiation of the vertical structure – plant height started to increase immediately after management stopped and most of the above-ground biomass moved higher from the near-surface position.

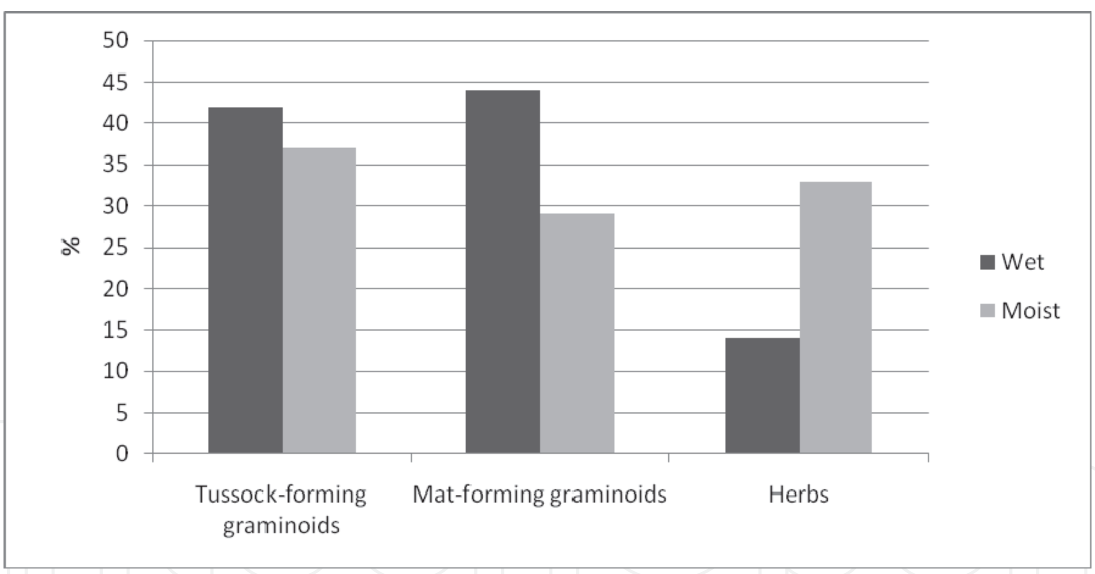

Fig. 1. Life-form distribution on Soomaa (West Estonia) wet and moist floodplain meadows

The species composition and duration of this vegetation change depend on climatic and trophic conditions and hydrology, also on the ecological trait of plants and availability of diaspores. General trends, however, are: decrease in species richness, change in species composition, increase in vegetation height and above-ground biomass, and finally replacement of the herbaceous community by woodland. Re-location of most of the biomass to a higher level in the community as described by Falinska (1991, 1995) takes place if herbs dominate – on wet meadows at a drier site. No comparable data about composition and biomass change are available due to abandonment of seminatural hay lands and pastures. Just general trends in vegetation change can be followed.

Floodplain meadow type[2] English description of classification in Truus & Tõnisson, 1998	**Plant community**	**Above-ground biomass** (g m^{-2})	**Above-ground biomass, mean for community type** (g m^{-2})
Dry floodplain meadow	*Sesleria–Festucetum ovinaea*	150	80
	Seslerio–Nardetum	40	
	Thymo–Festucetum	30–100	
	Sieglingo–Nardetum	40–80	
	Anthoxantho–Agrostetum	40–100	
	Galio–Agrostetum tenuis	50–150	
Moderately moist floodplain meadow	*Agrostetum giganteae*	150–250	200
	Deschampsio–Festucetum rubrae	100–300	
	Alopecuretum pratensis	150–380	
Moist floodplain meadow	*Cirsio–Polygonetum bistortae*	150–300	230
	Filipendulo–Geranietum palustris	200–400	
	Deschampsieto–Caricetum caespitosae	100–250	
	Elytrigieto–Alopecuretum arundinacei	150–300	
Wet floodplain meadow with tall grasses	*Stellario-Deschampsietum*	80–200 (300)	250
	Phalaroidetum	150–500	
Wet floodplain meadow with tall sedges	*Caricetum distichae*	200–250	260
	Caricetum acutae	100–450	
	Caricetum rostrato-vesicariae	100–450	
Floodplain marshes	*Seslerio-Caricetum paniceae*	40–100	125
	Caricetum paniceo-nigrae	50–150	
	Caricetum diandro-nigrae	50–180	
	Caricetum cespitoso-appropinquatae	100–200	
	Caricetum elatae	80–300	

Table 1. Mean above-ground biomass of plant communities of floodplain meadows. The analyses are means for Estonia representing seminatural hay meadows in 1978-1981[2]

Analysis of life-form distribution on Estonian floodplain meadows in periods with different management showed an increased proportion of tall herbs and graminoids instead of low herbs and graminoids in the 1960s when these areas were mostly regularly mown and the end of the 1990s when they were out of use (Fig. 2). The proportion of tall tussock-forming graminoids did not change. On floodplain grasslands these plants inhabit depressions with a higher water table and thereby were absent even in the former period.

[2] Krall, H., Pork, K., Aug, H., Püss, O., Rooma, I. & Teras, T. (1980). *Eesti NSV looduslike rohumaade tüübid ja tähtsamad taimekooslused*, ENSV Põllumajandusministeerium IJV, Tallinn. [In Estonian]

3. Above-ground biomass

3.1 Methods for standing crop estimation

Wheeler & Shaw (1991) calculated above-ground biomass as the biomass increment between April and September. In regions with a dormant season for herbaceous plants in winter, above-ground biomass (that also represents production per year) is in its maximum in the middle of summer, but before abundant flowering. In wetlands different flowering times can be noticed: the sedges usually stop growing and flower in May and June (Leht, 1999) while common reed continues growing up to the August. In all cases, biomass samples were air-dried before measuring. Standing biomass measured in its maximum is usually equalized with production.

3.2 Above-ground biomass of floodplain meadows

In the period of regular management, mean values for above-ground biomass of Estonian floodplain meadows measured from 80 to 260 g m^{-2}, varying largely between community types and even communities[2]. On unmanaged floodplain meadows those values are more than twice higher (Tables 2 and 3). Zobel & Liira (1997) presented biomass values from 300 to 600 g m^{-2} for West Estonian floodplain meadows of Sauga, Vaskjõe and Kasari (the lowest value on a dry site). High standard deviation in Tables 2 and 3 shows high variability of floodplain meadows vegetation discussed earlier. For comparison, in the Czech Republic *Molinio-Arrhenetheretea* above-ground biomass in a moist floodplain meadow was 300–350 g m^{-2} (Joyce, 2001). Values of above-ground biomass from the earlier (with regular hay cutting; Table 1) and later (without management; Tables 2 and 3) periods show an increase in standing crop that can be explained as a result of management cessation. Standing biomass also varied threefold (from 263 to 763 g m^{-2}) on floodplains in Soomaa, West Estonia (Truus & Puusild, 2009).

Floodplain meadow type English description in Truus & Tõnisson, 1998	**Above-ground biomass** (g m^{-2}, St.Dev in parentheses)
Dry	458 (148.6)
Moderately moist	493 (240)
Moist	350 (448.3)
Wet	(no data)
Wet with tall sedges	742 (70.3)
Floodplain marsh	376 (100.9)

Table 2. Mean above-ground biomass on the Kloostri landscape transect, West Estonia. Previous hay-meadow, abandoned over 15 years

Truus & Puusild (2009) studied the distribution of ecological groups (graminoids, herbs, low and tall growth-form) in relation to management cessation. The ecological group composition turned towards tussock-forming plants but the most obvious change was the increase in vegetation height (Fig. 2).

Unmanaged wetlands are dominated by powerful species (Wheeler & Giller, 1982; Truus, 1998; Truus & Puusild, 2009). On sites with a permanently high groundwater level *Deschampsia cespitosa* or *Carex cespitosa* form high tussocks while low-growing tussocks (*Nardus stricta*, *Festuca ovina*) spread on dry or moist managed grasslands. The abandonment

Floodplain meadow type English description in Truus & Tõnisson, 1998	**Above-ground biomass** ($g\ m^{-2}$, St.Dev in parentheses)
Moist, regularly mown	572 (692.3)
Moist, mown, recently abandoned	333 (167.5)
Moist, unmown but mowing reintroduced	380 (178.2)
Moist, unmown over 15 years	763 (627.5)
Wet, regularly mown	263 (108.0)
Wet, mown, recently abandoned	516 (165.9)
Wet, unmown, but mowing reintroduced	452 (398.7)
Wet, unmown over 15 years	447 (86.4)

Table 3. Mean above-ground biomass on moist and wet floodplain meadows with different management regimes in Soomaa, West Estonia.

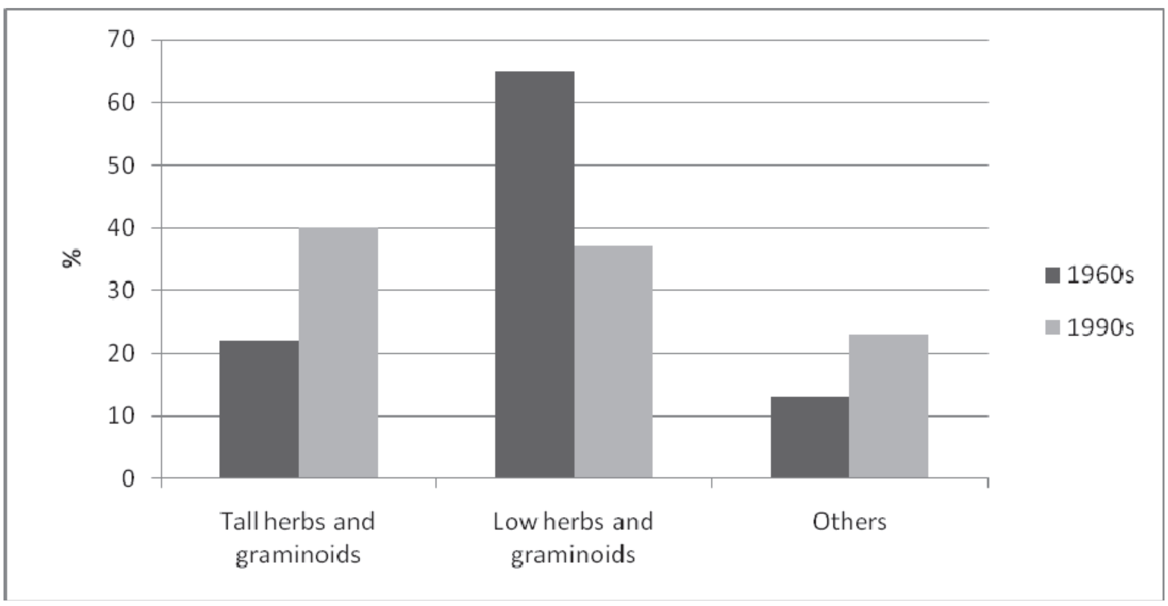

Fig. 2. Proportions of the most frequent growth-forms on floodplain meadows in periods of extensive management (first half of the 20th century) and unmanagement (end of the 1990s)

of grasslands can lead to dominance (in some cases to almost monospecies communities) of tall herbs like *Filipendula ulmaria*. The coverage and height of tussocks of *Molinia cerulea* increase on rich fen meadows (Ilomets et al., 2010).

3.3 Biomass of fens

Fen vegetation presented in Table 4 is highly variable and the biomass values vary between locations. The above-ground biomass values for low-growing vegetation range from 50 to 500 $g\ m^{-2}$ and from 600 to 1750 $g\ m^{-2}$ for both tall graminoids and tall herbs. For comparison, in Canada and adjacent USA mean above-ground biomass was 337 ± 142 $g\ m^{-2}$ for fens and bogs, and 924 ± 463 $g\ m^{-2}$ for marshes and swamps (Campbell et al., 2000).
No recent data are available on biomass production on fens in Estonia. The data from 1977–1980 (Table 4) gives very low values (50 $g\ m^{-2}$) for above-ground biomass of fen meadows.

The utilization of fen meadows grew in Estonia at the beginning of the 20th century. An experiment from 1922–1926 showed the yield of 140 to 450 g m^{-2} from unfertilized fen meadows.[3]. It was also mentioned that during the experiment hay production was related to weather conditions but decreased year by year (probably because of experimental hay cutting).

Location	**Vegetation community**	**Dry standing biomass (g m^{-2}) St.Dev. in parentheses**	**Reference**
England and Wales	*Schoeno–Juncetum*	~ 200	Wheeler & Shaw, 1991, Fig. 1
England and Wales	*Acrocladio–Caricetum*	~ 200	
England and Wales	*Potentillo–Caricetum*	~ 200	
England and Wales	*Peucedano–Phragmitetum*	~ 300	
England and Wales	Rich-fen meadow	~ 500	
England and Wales	*Cladio–Molinietum*	~ 600	
England and Wales	*Peucedano–Phragmitetum*	~ 700	
England and Wales	*Angelico–Phragmitetum*	~ 850	
England and Wales	*Cicuto–Phragmitetum*	~ 1200	
England and Wales	*Phragmites* consociation	~ 1300	
England and Wales	*Glyceria maxima* community	~ 1500	
England and Wales	Tall herb fen	~ 1750	
England and Wales	*Phalaris arundinacea* community	900–1200	Smith et al., 1985
England and Wales	*Glyceria maxima* community	700–1200	
Siberia, Russia	*Carex*–dominating fen	200	Pjavtšenko, 1967
Switzerland	*Saxifraga hirculus* fen	152–231	Venterink & Vittouz, 2008
Netherlands	*Molinietalia* fen	~ 300–400	Van der Hoek & Sýkora, 2006
Estonia	*Drepanocladо–Schoenetum*	50	Data from 1977-1980[2]
Estonia	*Seslerio–Caricetum paniceae*	50	

Table 4. Above-ground biomass of fens with highly variable composition in different regions

[3] Rinne, L. (1927). Sooheinamaa toodangu kahanemisest väetuse puudusel. *Eesti Sooparanduse Seltsi teated*, Vol.8&9, 3–15. [In Estonian]

4. Conclusions

Vegetation of floodplain meadows and fens varies depending on the environmental (soil, water) conditions and management regime. Both vegetation types have been in economic use but a great part of them is in the successional stage due to abandonment.

On low-productive sites plant species richness is primarily limited on abiotic conditions (WL, WLA, mineral content of soil and water, availability of plant nutrients).

The main limitation in highly productive sites is competition for light. Tall graminoids or herbs compete out low-growing plants, enabling even the development of monospecies vegetation.

The management status determines plant species richness and the above-ground biomass production. Above-ground standing biomass varied threefold due to management cessation on West Estonian floodplain grassland. Widespread cessation of management on seminatural meadows is a key for interpretation of different above-ground biomass values from different periods. Fen vegetation is probably more sensitive to above-ground biomass cutting than floodplain grassland vegetation.

It is complicated to predict species richness from community biomass, and biomass (or production) from site conditions.

Values of above-ground biomass increase from north to south but the geographical latitude (availability of photosynthetic radiation) is not as strong determinant for biomass production of wet grasslands as the local hydrological, nutritional and management status.

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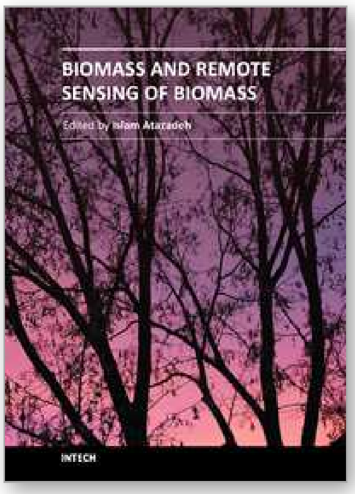

Biomass and Remote Sensing of Biomass

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Generally, the term biomass is used for all materials originating from photosynthesis. However, biomass can equally apply to animals. Conservation and management of biomass is very important. There are various ways and methods for biomass evaluation. One of these methods is remote sensing. Remote sensing provides information about biomass, but also about biodiversity and environmental factors estimation over a wide area. The great potential of remote sensing has received considerable attention over the last few decades in many different areas in biological sciences including nutrient status assessment, weed abundance, deforestation, glacial features in Arctic and Antarctic regions, depth sounding of coastal and ocean depths, and density mapping. The salient features of the book include:
Several aspects of biomass study and survey
Use of remote sensing for evaluation of biomass
Evaluation of carbon storage in ecosystems
Evaluation of primary productivity through case studies

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